The Growth Responses of Fish to Differences in Acidity-Related Lake Characteristics and Fish Species Composition

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Academic dissertation

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ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Raitaniemi, J., Rask, M. & Vuorinen, P.J. 1988. The growth of perch, *Perca fluviatilis* L., in small Finnish lakes at different stages of acidification. Annales Zoologici Fennici 25: 209–219.

II Raitaniemi, J. 1995. The growth of young pike in small Finnish lakes with different acidity-related water properties and fish species composition. Journal of Fish Biology 47: 115–125.

III Raitaniemi, J., Malinen, T., Nyberg, K. & Rask, M. 1999. The growth of whitefish in relation to water quality and fish species composition. Journal of Fish Biology 54: 741–756.

IV Raitaniemi, J. & Rask, M. 1994. Observations on the development of fish populations in small acidified lakes in southern Finland during a four-year period after liming. In: Müller, R. & Lloyd, R. (eds.): Sublethal and chronic effects of pollutants on freshwater fish. FAO, Fishing News Books, University Press, Cambridge. pp. 326–336.

V Rask, M., Vuorinen, P.J., Raitaniemi, J., Vuorinen, M., Lappalainen, A. & Peuranen, S. 1992. Whitefish stocking in acidified lakes: ecological and physiological responses. Hydrobiologia 243/244: 277–282.

VI Raitaniemi, J., Bergstrand, E., Fløystad, L., Hokki, R., Kleiven, E., Rask, M., Reizenstein, M., Saksgård, R. & Ångström, C. 1998. The reliability of whitefish (*Coregonus lavaretus* (L.)) age determination — differences between methods and between readers. Ecology of Freshwater Fish 7: 25–35.

Jari Raitaniemi took part in the field work of every paper and wrote the scripts with the exception of paper V, the script of which he commented on.

ABSTRACT

The main objectives of this study were to examine the growth of fish in lakes changed by acidification or acidification and liming; second, to clarify the abiotic and biotic factors that affect the growth of fish in these environments and third, to examine the effects of two alternative methods tested to mitigate the harmful effects of acidification; ie. liming and stocking with whitefish. An essential method in the study of growth patterns of fish, ie. age determination from calcified structures, was examined and the effects of possible age determination errors were discussed.

In acidified lakes of southern Finland, the growth rate of fish is at least occasionally retarded by physiological effects of acidity, but usually these direct effects on growth are indistinguishable. Either the growth rate is not affected because of adaptation or the stress effects are masked by biotic interactions such as competition or availability of suitable food organisms.

As a result of acidification, reproduction of fish fails and population densities decrease. The growth of perch is most clearly affected at a late stage of acidification ($pH < 5$), when the only fish remaining are those in the sparse populations of perch and possibly pike. The few perch have plenty of food, and they can grow remarkably fast. Despite their good tolerance to acidity, pike suffer from lack of small fish, and they may grow slowly. However, if they find something to displace fish food, they are likely to grow normally at least during their early years of life. Whitefish tolerates acidity, though not as well as perch, but better than roach. The growth of whitefish was faster in lakes without roach than in lakes that had thriving roach populations.

When liming is properly conducted, acid-sensitive fish species like roach can be restored. In the first years after liming, the growth rate of roach will usually rise and exceed the pre-liming conditions. The fisheries value of pike may also increase as roach is restored. From the viewpoint of fisheries, the result can be unwanted, if roach practically wipes out perch that is regarded as a more valuable catch. In lakes with $5 < pH < 6$ and sparse or missing roach, whitefish stocking can be successfully used in mitigating the deleterious effects of acidification on fisheries.

The two age determination tests indicated that ageing is most reliable, when the reader has all the information available of the fish under examination. The reliability of the age determination results will improve, if they are supported by other observations; for example, validation of ageing with known-age fish, length distribution, shape and composition of the calcified structures, or regular observations of the calcified structures of the population.

CONTENTS

INTRODUCTION

Background

In this century, acidification due to airborne, acidic pollutants has caused great damage to fish populations in Scandinavia and North America, for example (Almer et al. 1974, Beamish & Harvey 1972, Schofield 1976, Magnuson et al. 1984, Henriksen et al. 1989). In the early 1920s, a decline in fish populations was noticed in Norway (Muniz 1984), where brown trout *Salmo trutta* L. is the most affected fish species. Of brown trout alone, roughly 8200 populations have vanished and some 3900 are at risk (Hesthagen et al. 1999). Thousands of lakes and watercourses and their fish populations have suffered from acidification in Sweden (Henrikson & Brodin 1995). In Finland, fish stocks have been affected in poorly buffered small lakes of some sensitive areas, in particular (Rask & Tuunainen 1990). In 1995, the number of affected populations was estimated to be 2200–4400, and 1000–2000 of them had probably disappeared (Rask et al. 1995). The endangered populations were mostly roach *Rutilus rutilus* (L.) which is among the most acid-sensitive species (eg. Tuunainen et al. 1991, Degerman & Lingdell 1993, Vuorinen et al. 1994). Perch *Perca fluviatilis* L., the most common fish species in Finland, tolerates acidity well. Thus, only 15% of the damaged fish populations were estimated to be perch (Rask et al. 1995).

Changes in a lake ecosystem undergoing acidification

As pH decreases, species diversity decreases as well, and the number of species begins to decline at a pH level of about 6.0 (Appelberg et al. 1993). The numbers of algal species are reduced, but some acid-resistant algae, attached algae in particular, and *Sphagnum* mosses that are favoured by the form of the available organic carbon present in acidic water can become increasingly accumulated when pH < 5 (Hendrey et al. 1976, Overrein et al. 1980). The productivity of the ecosystem and decomposition of organic matter have been observed to decrease in acid lakes, and recycling of nutrients may be reduced as well (Hendrey et al. 1976, Overrein et al. 1980, Appelberg et al. 1993). The number of zooplankton species has been found to correlate with pH and to drop in acid lakes (Almer et al. 1974, Overrein et al. 1980, Havens 1991).

The abundance or absence of fish predators and differences in physiological tolerance are probably the most important factors producing the dominance patterns of zooplankton in acid lakes. Similarly, aquatic insect species have been on the decrease, and snails and mussels have gone down (Overrein et al. 1980). Among larger crustaceans, water louse *Asellus aquaticus* tolerates acidity exceptionally well, and it can still be found in some lakes with pH 4.8 (Overrein et al. 1980). The density of acid-tolerant invertebrates like *Asellus* or invertebrate predators such as water bugs (Corixidae), water beetles (Dytiscidae), dragonflies (Odonata), or phantom midges *Chaoborus* is mainly regulated by the abundance of fish, ie. fish predation, and these invertebrates (excluding *Asellus* in the most acidic lakes) can become remarkably abundant in lakes empty of fish (eg. Eriksson et al. 1980, Rask et al. 1996). In fact, many structural changes reported from acidified lakes may be attributed to altered predator-prey interaction after the decline in fish populations and should not be regarded as direct pollution effects (Eriksson et al. 1980).

In addition to acidity, the organisms of acid lakes are usually stressed by elevated concentrations of heavy metals and particularly aluminium that has been found to increase the toxicity of an acid water (Dickson 1978). To some extent, humic substances can protect the organisms by forming complexes with aluminium. In lakes with 4 < pH < 5, however, humic substances are usually precipitated by aluminium and transparency is increased (Dickson

1978). Abiotic variation has a strong impact on all trophic levels and it affects both top-down and bottom-up forces (Appelberg et al. 1993).

Effects of acidity and fish species composition on fish

Physiological effects of acidity

In acid stress of fish, the equilibrium between loss and active uptake of ions is disturbed, often followed by a decline in body Na^+ and Cl^- content (Leivestad et al. 1980, Rask & Virtanen 1986, Vuorinen et al. 1990). Plasma glucose concentration of whitefish *Coregonus lavaretus* (L.) has also been found to raise (Vuorinen et al. 1990). In brown trout, Cl^- loss was greater than Na^+ loss in both nature and tank experiments (Leivestad & Muniz 1976, Leivestad et al. 1980). In the plasma of female perch, decreased Ca^{2+} concentrations and increased haematocrit values have been observed (Vuorinen et al. 1992). In addition, changes in brook trout *Salvelinus fontinalis* (Mitchill) and whitefish gill morphology (Chevalier et al. 1985, Vuorinen et al. 1990, Peuranen et al. 1993), hyperventilation in brown trout and brook trout, and increased standard metabolism in brown trout have also been discovered (Rosseland 1980).

Recruitment failure of fish is probably the most important reason for declines in fish populations in acid waters (Rosseland et al. 1980), and it can occur for a number of reasons: a failure of fishes to spawn (Beamish et al. 1975) or a delayed spawning (Vuorinen & Vuorinen 1991, Vuorinen et al. 1992), difficulties in fertilization (Urho et al. 1984), or mortality of eggs or fry (Rosseland et al. 1980). In perch, newly hatched fry were the most sensitive to acidity (Rask 1984).

Of the fish species typical to Finnish small lakes, roach is clearly the most acid-sensitive. Population effects are found in pH 5.5–6.0, and roach usually disappears when pH < 5.5 (eg. Tuunainen et al. 1991, Degerman & Lingdell 1993, Vuorinen et al. 1994). Others from more sensitive to less sensitive are: other cyprinids (mostly as sensitive as roach), burbot *Lota lota* L., whitefish (usually stocked), ruffe *Gymnocephalus cernuus* (L.), perch, and pike *Esox lucius* L., of which the two last-mentioned can survive even if pH < 5.0 (Rask & Tuunainen 1990, Degerman & Lingdell 1993, Vuorinen et al. 1993, Vuorinen et al. 1994)

The growth of fish exposed to acid water has been shown to have reduced in experiments on perch (Rask et al. 1986) as well as salmonids such as rainbow trout *Oncorhynchus mykiss* (Walb.) and arctic char *Salvelinus alpinus* (L.) (Edwards & Hjeldnes 1977), brook trout (Kwain & Rose 1985), and whitefish (Rask et al. 1988). The growth of brook trout juveniles was found to rebound after retarding, in other words, the fish acclimated to low pH (Kwain & Rose 1985).

Ecological effects of acidity-related changes in lakes

As pH drops below 6, the density of roach decreases and the abundance of perch usually increases due to reduced interspecific competition (Appelberg et al.1992). After liming, roach may regain its dominance, which results in a decline in perch. Similarly, vendace *Coregonus albula* (L.) can regain its abundance and decrease the number of perch (Bergquist 1991, Appelberg et al. 1993).

In Swedish lakes where pH fell below 5, the population density of perch decreased, and this resulted in accelerated growth of perch (Almer et al. 1974, Hultberg 1985). The high growth rate was possible because of the increased densities of acid-tolerant invertebrates that are sparse in circumneutral lakes due to predation by abundant fish (Andersson 1972, Almer et al. 1974, Appelberg et al. 1993, Stenson et al. 1993). A prominent decrease in fish population density is usually followed by an increase in growth rate (eg. Le Cren 1958, Klein 1992, Valkeajärvi 1992, Salonen et al. 1997), although other simultaneous changes in environment may also lead to diminished availability of food and, consequently, growth rate (cf. Horppila & Peltonen 1997). Of naturally reproducing fish species, perch and/or pike have usually been the last ones surviving in the most acidic lakes (Degerman & Lingdell 1993).

Mitigation of the effects of acidification

Different measures have been taken to lessen the deleterious effects of acidification on fish populations. In Sweden, around 6300 acidified lakes and 6000 km of running water were limed before the year 1995 in a large-scale liming programme (Henrikson & Brodin 1995). The aim in liming has been to detoxicate the water for the continued existence or recolonization of natural flora and fauna. Chemically, this means raising the pH above 6.0 and alkalinity above 0.1 $mmoll^{-1}$ (Henrikson & Brodin 1995). In Sweden, post-liming growth of perch, char, and pike has usually been found to increase, and there is some evidence of good post-liming growth of whitefish, trout and roach, but a lack of pre-liming information (Degerman et al. 1995). The number of acidified waters with affected or vanished fish populations has been clearly smaller in Finland than in Norway or Sweden (Henrikson & Brodin 1995; Rask et al. 1995; Hesthagen et al. 1999), and no large-scale liming programmes have been carried out.

In small lakes of southern Finland, whitefish is usually not a naturally reproducing fish species. When stocked, however, it survives and tolerates acidity better than roach, for example (Rask et al. 1988, Vuorinen et al. 1994). In stocked whitefish, acidity does not seem to be as important in determining growth as some other factors, including stocking density, predation, competition, or general productivity of lakes (Rask et al. 1988).

Aims of the study

The objectives of the study were:

1) to get a picture of the growth of fish in lakes changed by acidification or acidification and liming (I–V),
2) to clarify the abiotic and biotic factors that affect the growth of fish in these environments (I–V),
3) to examine the effects of two alternative methods tested to mitigate the harmful effects of acidification; ie. liming and stocking with whitefish (IV–V).

To achieve these goals, the growth rates of perch, pike, and whitefish were examined in lakes with different abiotic and biotic characters (I, II, III). Eight lakes were chosen for the study of the impact of liming, including growth responses of perch and roach (IV), and six acidified lakes were stocked with one-summer-old whitefish to be regularly fished afterwards (V).

An essential method in the study of growth patterns of fish, age determination, was examined in two whitefish age determination tests (VI). In addition to the reliability of ageing, the possible effects of age determination errors on fish population studies will also discussed here.

MATERIAL AND METHODS

Lakes in the study

Most of the lakes in the studies I–V belong to the group of 80 lakes included in the Finnish Acidification Research Programme (HAPRO) — small headwaters, often surrounded by rocky coniferous forests and bogs that may have been ditched (Fig. 1, table 1).

The small drainage area and poor calcium content of the bedrock make these oligotrophic or dysoligotrophic lakes especially vulnerable to airborne acidification. In addition, pike material from 16 small lakes in the Evo State Forest area was used (II, Rask & Metsälä 1991, table 1), as well as whitefish material from three large Ostrobothnian lakes (Lappajärvi, Evijärvi, and Alajärvi) and two basins (Enonselkä and Kajaanselkä) of Vesijärvi, a large lake in southern Finland (III, table 1). The eutrophic Enonselkä basin of the last-mentioned lake was restored by biomanipulation, during which the main part of roach and smelt *Osmerus eperlanus* (L.) biomass was removed (Horppila & Peltonen 1994, Horppila et al. 1996).

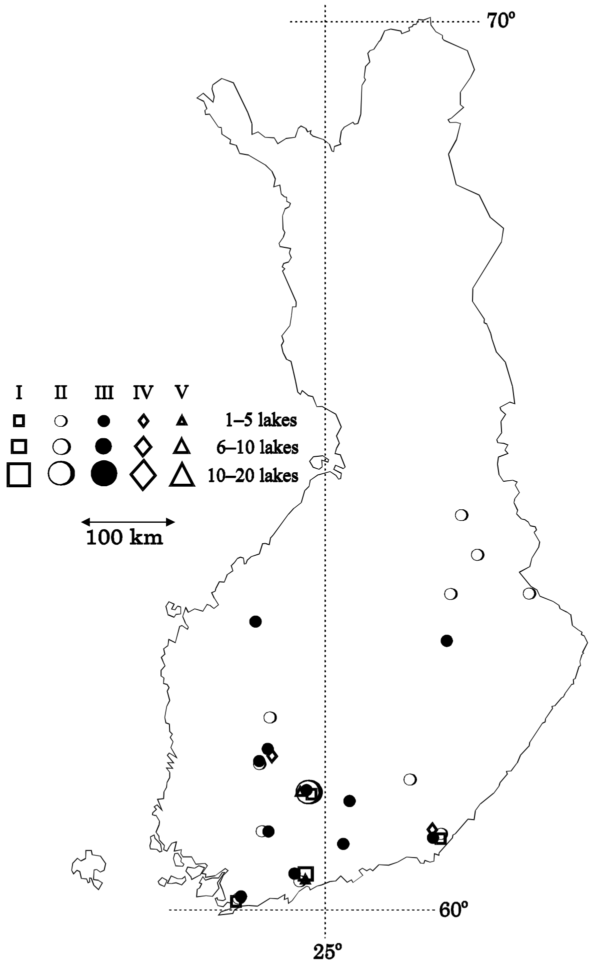

Figure 1. Locations of the lakes used in papers I–V.

In the small lakes, the most common naturally reproducing fish species were perch, pike, ruffe, and roach. Whitefish was also found in the catches of several lakes as a result of stocking (I–III). There were more fish species in the large lakes than in the small lakes (III, table 1). Paleolimnological (diatom analysis) and chemical (conductivity–alkalinity method) studies have indicated that the pH of the most acidic lakes began to decrease during the 1950s or 1960s (Tolonen & Jaakkola 1983, Kämäri 1985, Tulonen 1985, Tolonen et al. 1986).

According to local informants, roach disappeared or became rare in one of the lakes, Pieni Lehmälampi, as early as in the 1940s.

Eight small acidified lakes that were limed in southern Finland in 1986 and 1987 were chosen for a closer examination of the effects of liming (IV). Before the liming, their summer-pH was mostly 5.3–5.5 and alkalinity 0.00–0.03 $mmoll^{-1}$. After the liming, the summer-pH in the lakes was 6.0–7.0 and alkalinity 0.04–0.16 $mmoll^{-1}$. The six lakes selected for the whitefish stocking experiment were at different stages of acidification with pH 4.5–6.0 (V).

Table 1. Lake characteristics of 80 HAPRO lakes (I–III, V), 16 lakes from Evo area (II), five large lakes or basins (III), and eight limed lakes (IV). The number of fish species is counted from test fishing catches except in the large lakes (Granberg et al. 1989, Tammi et al., unpublished).

Character	HAPRO lakes			Evo lakes:		
	mean	min	max	mean	min	max
area (ha)	20	1	110	9	0.3	45
pH	5.7	4.4	7.6	6.0	4.9	6.6
alkalinity ($mmoll^{-1}$)	0.05	0.00	0.37	0.08	0.00	0.22
conductivity (mSm^{-1})	3.1	0.8	5.7	3.4	1.8	5.1
colour (mg Ptl^{-1})	25	0	90	141	13	320
Al_{tot} (μgl^{-1})	107	0	324	-	-	-
Number of fish species	3	1	6	4	2	8

Character	Large lakes:			Limed lakes:		
	mean	min	max	mean	min	max
area (ha)	5018	1090	14200	25	4	72
pH	7.1	6.5	7.8	6.5	6.0	7.0
alkalinity ($mmoll^{-1}$)	0.31	0.14	0.54	0.08	0.04	0.16
conductivity (mSm^{-1})	8.6	5.1	11.5	3.3	2.3	3.9
colour (mg Ptl^{-1})	67	10	185	36	10	80
Al_{tot} (μgl^{-1})	-	-	-	100	12	228
Number of fish species	17	12	19	4	3	5

Water chemistry

The lakes were sampled for water chemistry during summer stratification (I–V), excluding nitrogen and phosphorus contents that were taken during autumn or spring turnover (II–III) and the Ostrobothnian lakes that were sampled during the autumn turnover (III). The water samples were taken from the depth of 20 cm or 1 m, and they were analysed according to the Finnish standard methods for water analysis (SFS standards). The samples from HAPRO lakes were analysed in the laboratory of the Finnish Game and Fisheries Research Institute (I–V), excluding nitrogen and phosphorus contents which, like the samples from the Ostrobothnian lakes, were analysed in the laboratories of the Finnish Environment Institute (former the National Board of Waters and Environment; II, III). The samples from the 16 lakes in the Evo State Forest Area were analysed at the Lammi Biological Station, University of Helsinki (II) and the samples from Vesijärvi in the Lahti Research Laboratory (III).

Fish samples

The fish were caught from the HAPRO lakes by test fishing with a series of eight 1.8 x 30 m gill nets (12, 15, 20, 25, 30, 35, 45, and 60 mm bar mesh size) at depths of 2–4 m, each lake sampled one to five times (I–V). Wire traps with 1 cm square mesh were used to catch perch from Valkea Mustajärvi (I) or pike from Evo lakes along with gill nets and angling (II). In the six lakes stocked with whitefish, gill nets with mesh sizes 12, 15, 20, and 25 mm (bar length) were used in June and October, 1987 (V). The whitefish from the large lakes were sampled randomly from the fishermen’s catches, or the whole whitefish catch of the fishermen was bought. In addition to gill nets, the fishermen in Lappajärvi used pound net and in Vesijärvi seine and trawl (III). The mean gill raker number of the whitefish included in the studies was 50–55 (the whitefish form also called *C. l. pallasi*). In the basins of Vesijärvi, two whitefish forms with an equal growth rate and mean gill raker numbers of 42–45 and 55 were included.

The fish in the gill net catches were counted and weighed, and a random sample (I, III) or an equal number from different length groups (1 cm accuracy; III–V), or a sample from other fishing gear (I–III) was taken to individual measurements of total length and weight and the determinations of age and growth.

For age and growth determinations, opercular bones were taken from perch (I, IV), cleithral bones from pike (II), and scales from roach (IV). Scales were taken from the whitefish caught from small lakes, and scales, otoliths (sagitta), and in most cases opercular bones as well, from the whitefish caught from large lakes (III, V).

Age and growth determinations

The age was determined and growth back-calculated from the opercular bone of perch and whitefish (I, III, IV), the cleithral bone of pike (II, Casselman 1990), and the scale of roach (IV) and whitefish (III). In addition, the otolith was used in the age determinations of whitefish from the large lakes (III), observing the methods described in Raitaniemi (1997) and paper VI. In the back-calculation, the Monastyrsky’s procedure was followed with the exception of roach for which the procedure of Fraser and Lee was used (Bagenal & Tesch 1978).

In cases where the estimated lengths of the sexes at the studied ages were compared (I–III), the differences were not statistically significant. Thus, the sexes were combined in the examinations.

Comparisons of growth

The relationships between growth and abiotic and biotic factors, or fish growth before and after liming, were examined by dividing the lakes or fish into different groups on a chemical and/or biological basis (I–V) and comparing the groups with the Student’s t-test or Mann-Whitney U-test (I–V), one-way ANOVA, repeated measures ANOVA, or using grouped variables in the Spearman’s correlation test (III). Finally, correlations (Pearson or Spearman) between the growth rate of fish and abiotic or biotic factors were tested (I–III).

Age determination as a basis for growth estimations

Two different age determination tests were carried out on whitefish material by several readers (VI). In the first one, age was determined separately from scales, otoliths and opercular bones, and in addition, three different populations were mixed in the samples to prevent the readers from making presumptions of the calcified structures. In the second test that was made on known-age individuals, the readers got scales and otoliths at the same time with additional information about the fish, and all individuals were from the same lake. In addition to different aspects in the reliability of ageing, the effects of ageing errors on age distributions and growth estimates from the mean lengths of fish were studied.

RESULTS AND DISCUSSION

Effects of acidity and fish species composition on fish growth in lakes

Perch

The most obvious effects of acidity on perch growth were indirect in the majority of the acidified lakes. The growth rate of perch correlated negatively with pH, the correlation being clearest in the second year of life. The increased growth rate of perch was most evident in lakes that were not only among the most acidic, but also where the numbers of fish in the catches were among the lowest (I). Low fish densities were confirmed in mark-recapture and roe rearing studies by Lappalainen et al. (1988), who found out that the perch density in lakes with pH < 5 was only 0–250 ha^{-1} compared with the density in circumneutral lakes, 1400–3300 ha^{-1}, and that this difference in densities was caused by failures in reproduction. Indirectly, the failures in reproduction were also seen in the length and age distributions of the catches from the most acid lakes, where young fish were often exceptionally rare or lacking (I). An increased growth rate of perch or yellow perch *P. flavescens* Mitchill in acidified lakes has also been detected by eg. Ryan and Harvey (1980) and Hultberg (1985). Correspondingly, a marked increase in the growth rate was observed by Rask et al. (1996) in a lake basin where less than 3% of the perch population survived in an almost total fish kill.

A drastic decrease in fish density is followed by exceptionally low or even negligible predation on planktic and benthic invertebrates by fish. In an acid lake, this gives acid-resistant species a chance of increasing their densities from what is usual in lakes populated by numerous fish. The numbers of eg. water bugs, phantom midge larvae, dragonfly larvae, water beetles, and water lice may increase (Andersson 1972, Almer et al. 1974, Appelberg et al. 1993, Stenson et al. 1993). In Orajärvi, a lake where the growth rate of perch was one of the fastest, a scuba diving in May 1992 revealed that in the depth of 2–3 m, water lice were remarkably numerous on the bottom and easy for the diver to catch, not to mention perch (Nyberg et al. 1995). In the catch of the test gill-netting in 1985, even the largest perch of Orajärvi had their stomachs filled with water lice (I). The growth rate of these water louse feeders in Orajärvi resembled that of piscivorous perch in large lakes (Smirnov 1977, Le Cren 1992), though not having a ‘double’ growth curve described by Le Cren (1992) — an increase of already slowed growth rate as the perch start to feed on fish. The growth rate of perch decreased when the Orajärvi population was recruited by more young perch and the population density increased in the first half of the 1990s, (Nyberg et al. 1995).

In another acid lake, Pieni Lehmälampi, the fast growth rate began to slacken after the perch had reached the age of 3–4 years and the length of about 20 cm, which was still high for that age (I). A corresponding decrease in growth rate has been observed by Ryan & Harvey (1980) and Hultberg (1985) and it is possibly related to the availability of only small-sized invertebrate food for the large perch and/or to the effects of acid stress, like an increased food demand. More indication of acid stress was found in the individuals from Hauklampi — they had not grown as fast as the perch from the other acid lakes with sparse populations, but still faster than the individuals from lakes with pH above 5 (I). Hauklampi had by far the highest total aluminium content, 400 $\mu g l^{-1}$, compared with values above 200 $\mu g l^{-1}$ in other highly acidic lakes. In Norway, acid stress was also suggested to be the reason for the lacking growth response of perch and brown trout to reducing population density (Rosseland et al. 1980).

The slowest back-calculated growth rates of perch in the second year of life were found in two lakes with high pH and strong roach populations, Iso Mustajärvi and Kotilampi, and in Iso Mustajärvi in the first year of life as well (I). Of the lakes in paper I, these were the only ones with alkalinity above 0.10 $mmol l^{-1}$ (0.19 and 0.13 $mmol l^{-1}$, respectively), and in number, the catch of roach in Iso Mustajärvi (506 individuals) was larger than in the other lakes with roach in their catches (1–144 individuals). In addition, the higher alkalinity and lower mean weight of roach in Iso Mustajärvi (mean weight 21 g) and Kotilampi (mean weight 25 g) suggest that their roach populations were denser than those in Kattilajärvi (mean weight 44 g) and Vitsjön (mean weight 77 g). Interspecific competition by strong roach populations may have contributed to the slower growth of perch in Iso Mustajärvi and Kotilampi. The retarding effect of roach on the growth rate of 0+ perch was detected in small lakes stocked with roach (Byström et al. 1998) and on the growth rate of 0+ and 1+ perch in enclosures (Persson & Greenberg 1990), as well as on the growth rate of 1+, 2+, and 3+ perch in a lake where the majority of roach had been removed (Persson 1986).

Pike

No relationship between pike growth and acidity was observed (II). Although pike can tolerate acidity well (I, II, Muniz 1984, Rask & Tuunainen 1990, Vuorinen et al. 1994), it may have problems in acid lakes. Besides possible failures in reproduction (Vuorinen et al. 1993), the pike in very acid and practically fishless lakes may have difficulties in finding suitable food and, as a consequence, grow slowly (Hultberg 1985, Rask & Tuunainen 1990). Because of the joint effects of decreasing recruitment and lack of suitable food, some pike populations may have disappeared from acidic lakes. In the Finnish test gill-nettings conducted in 66 lakes in the summers of 1985 and 1986 (Tuunainen et al. 1986, 1987), pike was present in an exceptionally small proportion of catches from lakes with pH < 5 (13%, n = 15) when compared with lakes with 5 pH 6 (51%, n = 37) or pH > 6 (57%, n = 14) (χ^2-test, $\chi^2 = 7.520$, $p < 0.05$).

Despite the shortage of small fish, the few pike in otherwise practically fishless lakes were found to be able to grow normally in the first years of life, probably feeding on invertebrates, frogs etc. (II). However, it is obvious that at an older age, invertebrates are not sufficient for a good pike growth.

A statistically significant positive relationship was discovered between the growth in the first year and water colour, and pike growth was better in lakes with roach present than in lakes without roach (II). Significant correlations were also found between pike growth and nitrogen and phosphorus contents, but in partial correlation, only the correlation with water colour remained significant. In lakes with strong roach populations, the correlation was even stronger than in all the lakes of paper II between the first summer growth of pike and water colour ($r = 0.70$, $p < 0.001$, $n = 20$). In lakes without roach, no correlation was found (II).

The highest correlation between pike growth and colour could be explained by temperature that may be higher in humic than in clear waters near the surface where small pike live during the growing season (cf. Rask & Arvola 1985). Because of the higher temperature, the pike in humic waters might be able to seek their way into an optimal temperature and grow faster than in colder conditions (cf. Casselman 1978, Bry et al. 1991). This was supported by the negative correlation between the first year growth of pike and lake area in lakes < 20 ha (II). The effects of temperature on pike growth, in general, can also be seen when comparing the growth in different parts of Europe with the northern waters of Finland (II).

The presence of a strong roach population probably improved the availability of suitable prey for the small pike (cf. Eklöv & Hamrin 1989) and enabled a faster growth than in lakes without roach (cf. Mann & Beaumont 1990). In roach lakes, the good availability of prey possibly enabled the more apparent relationship between growth and water colour, or growth and temperature.

Whitefish

Contrary to what could be expected from laboratory or tank studies, the growth of one-year-old whitefish correlated negatively with several water characteristics: conductivity, calcium content, P_{tot}, alkalinity, pH and colour (III). Despite the correlations with water characteristics, the growth of young whitefish in the first summer after stocking, ie. in the second year of life, was not found to be directly related to chemical water characteristics. The whitefish had the best growth rate in the lakes from which roach had disappeared because of acidity. In these lakes, perch and ruffe were usually still present. As an opposite to the fastest growth in lakes without roach, the slowest growth was observed in lakes with strong roach populations (III). In partial correlation, the relationship between whitefish growth and roach density remained when the other variables were kept constant. When roach density was kept constant, the relationships between whitefish growth and water characteristics became non-significant (III).

As with perch, the increased growth rate of whitefish in acidified lakes was due to lowered densities of natural fish populations and decreased competition for food. The major difference between whitefish and perch is that in stocked whitefish with moderate population densities, the part of competition that decreased was interspecific instead of being both inter- and intraspecific like in perch populations (I, III). The results indicate that there is competition between whitefish and roach in small lakes at least in the second summer of whitefish life. In large lakes, the competition with vendace may retard the growth of indigenous whitefish as early as in the first year of life, and this effect can still continue in the second year of life (Heikinheimo-Schmid 1992, Haakana et al. 1997). In whitefish released at the age of one summer, the growth effects of changes in vendace density can be detected in the first year growth in the lake, ie. the second year of life (III). Roach and vendace are probably competing with the young whitefish for zooplankton resources, as roach is an effective planktivore (Langeland & Nøst 1995), not to mention vendace that is primarily planktivorous throughout its life (Viljanen 1986). In a Norwegian whitefish–pike lake, the introduction of roach led to a great decline in the whitefish population (Langeland & Nøst 1994). Competition by other fish species like smelt or other cyprinids is also possible (III).

In a Danish hypertrophic freshwater fjord, a large release of migratory, sparsely gill-rakered whitefish resulted in a different way from what could be expected from the results of studies on densely gill-rakered whitefish in Finland. Despite strong populations of cyprinids, the whitefish grew very fast in the fjord (Rasmussen 1990). The difference in whitefish forms may contribute to this deviation, but it is also possible that discrepancies in the environment have resulted in different relationships between the fish species. The fast growth of whitefish and the presence of very large roach in the fjord may suggest that there are some other factors than competition for food that limit fish densities.

As the size of the fish and feeding habits change, the competitive relationships also change. Since especially young whitefish are affected by interspecific competition with roach or vendace, intraspecific competition may often be the main reason for the retardation of growth in all age-groups or at an older age (Klein 1992, Valkeajärvi 1992). An increase in the growth rate of all age-groups of peled *Coregonus peled* Gmelin was observed in two populations after decreases in population density (Salonen et al. 1997).

In the studied lakes, no clear relations were found between the growth of the third or fourth year of whitefish and other studied variables. In the fifth year, however, the growth rate was positively related with the number of fish species, lake area, and conductivity of the water (III). Compared with the simple systems of small lakes, the complex systems of large lakes give whitefish a better chance of shifting from plankton to larger prey like amphipods, mussels, and even small fish (cf. Odenwall 1927, Nilsson 1979). This enables faster growth than in small lakes and is probably the reason for the positive relationship between the growth of older whitefish and two variables — lake area and number of fish species — both expressing the complexity of the ecosystem (III).

Efforts to lessen harmful effects of acidification

Liming

In the eight limed lakes, the effects of liming on water quality varied from small and transitory improvements to considerable changes in pH and alkalinity (IV). The impact of liming on fish populations was similarly varying; it was unnoticeable in some of the lakes, where the change in water quality was among the smallest, and drastic in one lake with the highest rise in alkalinity. In seven out of eight lakes, perch remained the dominant species in the catches. Six lakes were inhabited by acid-sensitive roach, the proportion of which increased in the catches of three lakes after liming. In one of them, Suurilampi, where alkalinity rose from 0.03 to 0.16 $mmoll^{-1}$, the few roach left before the liming had reproduced so effectively that four years after liming, roach was the dominating fish species that had practically displaced perch. In two of the three lakes with an increased number of roach, the roach were dominated by the year-class hatched just after liming. In one lake, Havisevanjärvi, especially the number of old and large individuals increased in the catch, which was in accordance with the experience of local anglers. Other fish species were represented by only a few individuals in the catches; thus, their proportions before and after liming could not be compared (IV). During the same years, no improvements were observed in the roach populations of non-limed lakes (Raitaniemi & Rask 1990, Rask et al. 1995).

The drastic rise in the number of roach in Suurilampi and minor effects in other lakes with a smaller decrease in acidity are accordant with eg. Almer et al. (1974), Hultberg (1985), Rask & Tuunainen (1990), and Tuunainen et al. (1991); a similar type of recovery of a roach population was described by Eriksson et al. (1983). The reason for the replacement of perch by roach is possibly the ‘juvenile bottleneck’ described by Byström et al (1998). In general, a displacement of perch by roach as drastic as that in Suurilampi is not typical in limed lakes (Degerman et al. 1992, Degerman et al. 1995). Besides acidity, the relationship of these species is probably associated with the productivity and morphometry of the lake and aquatic vegetation (cf. Persson 1991, Persson et al. 1991, Persson & Eklöv 1995). Concerning roach or other acid-sensitive species, in only two of the eight lakes, alkalinity rose to the level of 0.10 $mmoll^{-1}$, which is probably enough to protect the water from abrupt drops of pH (Wilander et al. 1995). Cyprinids which had disappeared did not return to one of these lakes, Kalliojärvi, during the study. The periods of high runoff, especially the time of snow melt in the spring, are the most critical to sensitive fish species in limed lakes (Bengtsson et al. 1980, Booth et al. 1986). Low pH and its consequences (eg. high aluminium content) in the spring probably affect the gonadal development of fish (Fromm 1980), which is possibly also the reason for delayed spawning detected in perch (Rask et al. 1990) and whitefish (Vuorinen & Vuorinen 1991) in acidified lakes. High mortality of eggs and fry is the final cause for failures in reproduction (eg. Gjedrem 1976, Kwain & Rose 1985, Cleveland et al. 1986, Tuunainen et al. 1991, Vuorinen et al. 1994).

Despite the protective complexation between aluminium compounds and dissolved organic carbon (Hutchinson & Sprague 1987), the decrease of aluminium content, maybe including labile aluminium, in the humic waters of Rukojärvi and possibly Havisevanjärvi as well, may have contributed to the increase in roach population, since the rise in pH and alkalinity in these lakes was only modest (IV). High aluminium concentrations have been reported to reduce the survival of newly hatched roach at pH 5.75, and high mean weight and low catch of roach, expressing failures in reproduction, were detected in a lake with pH close to 6 but with high aluminium concentration (Tuunainen et al. 1991, Vuorinen et al. 1994).

According to the back-calculations of growth, the growth rate of roach was faster after liming than before liming. The only exception among the lakes was Salminen, where the liming failed to improve the water quality. A different kind of exception was Havisevanjärvi, to which the increased old individuals had run from a larger lake downwards the lake system. The rise in their growth was very clear; in different individuals, it took place in different years after liming, probably indicating the year of arrival (IV). Already before the liming in 1985, an increase in the growth rate of old roach was detected in some individuals that had probably immigrated at that time (Raitaniemi & Rask 1990).

The increase in the growth rate of roach after liming may be a consequence of reduced acid stress (cf. Edwards & Hjeldnes 1977, Rodgers 1984, Vuorinen et al. 1990). It is also possible that in the roach born in the limed lakes, an increased number of planktic and benthic invertebrates or other organisms enabled the faster growth after liming (cf. Hultberg & Andersson 1982, Eriksson et al. 1983). In the roach that came into Havisevanjärvi, the increased availability of food was clearly the reason for the better growth rate.

In the perch of these lakes, the influence of temperature on growth was evident in the first year of life, but difficult to distinguish from the possible effects of liming. However, it seemed that liming also had a slight positive effect on the growth of young perch (IV). In Swedish limed lakes, the changes in the growth rate of perch after liming have followed changes in predator-prey relations and competition, being both positive and negative (Appelberg 1995a, Appelberg 1995b, Nyberg 1995).

From the viewpoint of recreational fishing, an extreme case such as practical displacement of perch by roach, is not an ideal change in the fish stocks. In Havisevanjärvi, however, the local fishermen experienced a positive change that was indistinguishable in the test fishings, probably because of the test fishing method used. The pike catches that were almost non-existent before liming improved 4–5 years after liming. Similar catches of pike had not been experienced after the beginning of the 1960s. The positive effects of roach on the feeding of pike were possibly the cause for the improvement (II). In Swedish limed lakes, pike is favoured by the presence of roach (Appelberg & Degerman 1991).

Stocking with whitefish

Whitefish stockings that were conducted in six lakes at different levels of acidity were successful in the least acid lakes with normal perch populations, Alinen Mustajärvi and Valkea Mustajärvi (pH 5.2 and 6.0, respectively; V). Despite acidity (pH 4.5) and high aluminium content (Al_{tot} 159 $\mu g l^{-1}$), the stocking was still successful and the growth of whitefish fairly fast in Iso Lehmälampi, where the original perch population had almost vanished before the lake was stocked with whitefish. However, only a few quickly grown whitefish were caught from Pieni Lehmälampi, whose water quality was quite similar to that in Iso Lehmälampi but which was populated by a sparse perch population, including a number of large specimens of 20–25 cm in length (V, Lappalainen et al. 1988). In two other acid lakes, Hauklampi that had a very high aluminium content (Al_{tot} 387 $\mu g l^{-1}$) and Vähä Valkjärvi that had one of the lowest pH-values, low conductivity, low colour, and low COD, the stocking failed completely; that is, no whitefish were recaptured (V).

When excluding the aspect of nature conservation, stocking with whitefish can be used as an alternative to liming in improving the fisheries value of an acidic lake, although natural reproduction of whitefish was not expected. Even in a lake with pH less than 5, whitefish may be able to survive and grow quickly to the size of several hundreds of grams (III, V). However, in lakes which are almost fishless because of acidity, acid stress may lead to the death of all released fingerlings, which probably happened in Hauklampi and Vähä Valkjärvi (V). If the lake is populated by a sparse population of large perch, results of whitefish stocking can also be doubtful. Large perch can be efficient predators, which they probably were in Pieni Lehmälampi (V).

It seems that lakes where whitefish stocking can most likely be expected to succeed, still have a normal population of small perch, and ruffe can be present as well (III). These two species do not compete with whitefish as much as roach does (III), although the possibility that whitefish reduce the growth of eg. young-of-the-year perch cannot be excluded (cf. Svärdson 1976, Byström et al. 1998). In the lakes that either do not have roach or where roach population is sparse and perch population dense, pH is usually from 5 to 6 (I, Rask & Tuunainen 1990, Rask et al. 1995). As in an acidic environment, an efficient removal of roach from a non-acidic lake may also improve the conditions of whitefish (III).

The examination of whitefish growth after the first year in the lake can be used fairly reliably as an aid in predicting the success of whitefish stocking, since the results of the growth study (III) agree with the whitefish catch results from different lakes by Salojärvi & Ekholm (1990). The most successfully stocked lakes in their study were the ones where the proportion of perch or perch, pike, and burbot in the catches was high, and the poorest results were from lakes where the roach, roach and vendace, or whitefish catches were high. Thus, when stocking moderately acidic lakes ($5 < pH < 6$) with whitefish, a higher stocking density than in circumneutral lakes on the average can be successfully used because of the lacking competition by roach (III).

Age determination as a basis for growth estimations

In the first age determination test on separately determined calcified structures of whitefish (scale impressions, otoliths, and opercular bones) from three different populations by three different readers, the precision of the readers was low both between readers and between different structures (VI). This may have partly been due to the fact that the calcified structures from the three populations had been mixed with each other. Still, it was clear that in the samples of slow-growing whitefish, the determinations made from otoliths showed older ages than the determinations from scales. The otolith ages were considered to be more accurate than scale ages (VI, cf. Casselman 1983, Beamish & McFarlane 1995).

In the second age determination test that was conducted on known-age whitefish and where both scales and otoliths were available to the eight readers, the results were better: 73–90% of the determinations were correct. The use of two calcified structures and the knowledge of the material were considered to improve the accuracy. It was found that even if 80% of the fish were aged correctly, an exceptionally strong or weak year-class could remain unidentified because of a bias in age determination. Growth estimates were considered less sensitive to ageing errors than age distribution, at least when growth is estimated from the mean lengths of the age-groups (VI).

In studies based on age determination, it should be perceived that erroneous determinations and, further, erroneous estimates of age distribution and growth rate can occur. Even a fairly small proportion of erroneous age determinations can be followed by a misleading estimate of age distribution (VI). The findings can be regarded as more reliable, if the age determination results are backed up by direct or indirect validation of the age determination method used. Other observations with matching results with those of the age determinations also increase the reliability of the age determinations.

The length distributions of perch in paper I support the trend in age distributions — the fish in the catches from the most acidic lakes (pH < 5) were on the average older than in the moderately acidic (5   pH < 6) or circumneutral lakes (pH ⇩ 6). The opercular bones in the perch from the most acidic lakes were also clearly different from the bones in the perch from less acidic lakes: thick, opaque, and large with broad annuli or ring structures (I). According to the study of Appelberg et al. (1998), the opercular bone is reliable concerning the first years of life, but when ageing perch older than 7–8 years from an opercular bone, age can be underestimated.

The positive relationship between the back-calculated first year growth of perch and the yearly mean air temperature in the growing season (IV), which has also been observed elsewhere with perch fingerlings caught from natural waters (Karås 1996), suggests that the first annulus of most perch had been determined correctly and their growth had been back-calculated comparably (IV).

In the pike growth study (II), uncertainties were caused not only by possible errors in age determinations, but also by the small numbers of pike per lake — a great variation in growth could have meant that no trends between pike growth and abiotic or biotic variables had been discernible. However, the presence of plausible and statistically significant relationships in the material suggests that the age determinations are mainly correct at least concerning the first years of life, or the first annuli.

The reliability in ageing whitefish was examined in different ways. The age of the individuals in paper V was known. The data of false rings and annuli in the scales of whitefish in paper V and in the known-age migratory whitefish in Raitaniemi (1997) provided the guidelines to the differentiation of actual annuli from other checks in the small scale samples of 11 lakes in paper III. Of these fish, actual ageing was not conducted because otoliths were missing (cf. VI, Ausen 1976, Barnes & Power 1984, Skurdal et al. 1985). However, back-calculation of growth in several years of life was possible. In the whitefish from the rest of the lakes, otolith and opercular bone were used in ageing in addition to scale according to the recommendations in paper VI and Raitaniemi (1997).

One way to increase the reliability of ageing is to observe regularly the growth of the calcified structures of fish in a certain population. This was possible with the roach from the limed lakes, particularly if the roach were born after liming, because the lakes were test fished every second year (IV). In older roach, the risk of error was higher.

SYNTHESIS

The growth rate of fish in Finnish acidified lakes may at least occasionally be retarded by acid stress, but usually direct effects on growth are indistinguishable. Either there are no stress effects because of adaptation or the stress effects are masked by biotic interactions; that is interspecific and intraspecific competition and the availability of suitable food organisms.

During the acidification process of a lake, roach is one of the first fish species to disappear. In perch, the end of interspecific competition with roach may increase the growth rate at an early age. In whitefish stocked as fingerlings, the disappearance of roach leads to decreased interspecific competition and clearly increases growth in the second year of life. Pike however, is affected in a different way. As roach fry vanish, pike fry have more difficulties in starting to feed on fish. As a result, the growth of pike in the first summer of life is slower in lakes without roach than in lakes with strong roach populations, and the pike population may also become sparser than earlier.

When pH decreases below 5 and aluminium content possibly also increases, the reproduction of perch will largely fail and the population density will decline. Among the remaining perch, intraspecific competition will decrease and the perch begin to grow rapidly to larger sizes, unless the water quality, eg. total aluminium content above 300 $\mu g l^{-1}$, strained the fish so much that they grow slowly despite abundant food. Pike have difficulties in finding fish food, and the pike population may completely disappear or the few pike survive feeding on invertebrates or other substitutes for fish. Depending on how these pike find food, they will either grow very slowly or even normally in the first years of life.

The harmful effects of acidification can be diminished by liming. When an adequate liming method is used, acid-sensitive fish populations can be restored. In the first years after liming, the growth rate of roach will usually increase from pre-liming conditions. Some results from Sweden and Finland suggest that the fisheries value of pike can increase as roach population is restored. From the viewpoint of fisheries, the result of liming can in some cases also be negative. Roach may almost wipe out perch that is regarded as a more valuable species for anglers than roach.

If the fisheries value is to be increased or maintained, stocking an acid lake with whitefish has a fair chance of success. In lakes with $5 < pH < 6$, where roach population is sparse or lacking and perch population consists of numerous small-sized perch, whitefish stocking can be profitable with even higher stocking density than what generally is recommended in stocking with whitefish fingerlings. When pH 5, the stocking is more risky. If there is a number of large-sized individuals in the perch population, whitefish stocking may fail because of predation. Even after the perch population has been wiped out, stocking with whitefish can be worthwhile and growth of the whitefish fast, although acid stress may be retarding the growth rate. Nevertheless, there is a considerable risk that the water is too toxic to the whitefish fingerlings and they will die soon after stocking.

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